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# THE VEGETATION OF SKOKIE MARSH, WITH SPECIAL REFERENCE TO SUBTERRANEAN ORGANS AND THEIR INTERRELATIONSHIPS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 155

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(WITH TEN FIGURES)

The work on which this paper is based was begun in the autumn of 1910 and was concluded in the autumn of 1911. The detailed study of subterranean organs was carried on chiefly in the summer of 1911. The writer gratefully acknowledges his indebtedness for many valuable suggestions and much helpful advice, to Dr. HENRY C. COWLES and to Mr. GEORGE D. FULLER, under whose joint supervision the investigation was pursued, and also to Dr. J. M. GREENMAN for certain taxonomic assistance.

Skokie Marsh<sup>1</sup> is intimately associated with Skokie Stream, a small, sluggish stream beginning west of Waukegan, Ill., and extending southeast to a point west of Glencoe, Ill. Because of interference by cultivation and by drainage, the areal limits of the marsh can be defined only arbitrarily. As shown in the accompanying map (fig. 1), however, Skokie Marsh is approximately 12 km. long and at its southern end becomes 1.5 km. wide.

In early postglacial times, the marsh was an embayment (ATWOOD and GOLDTHWAIT 1, p. 58), which later subsided, giving place to a system of drainage. At present the surface soil almost throughout the marsh consists of a black muck or partially decayed peat, 1 m. or less in thickness. Underneath is a subsoil of glacial clay.

## General features of the marsh vegetation

Upon analysis, the vegetation at Skokie Marsh is found to consist of three rather pronounced formations.<sup>2</sup> Along the course

<sup>1</sup> For many additional data and photographs of Skokie Marsh, see BAKER (2).

<sup>2</sup> The words "formation" and "association" are used throughout this paper in the sense accepted by WARMING (16).

taken by Skokie Stream, the plants constitute distinctly a reed swamp formation (fig. 2). Extending along on either side of the reed swamp is a broad level expanse, intermediate between reed swamp and meadow. This may be designated swamp meadow (fig. 3). At the outer edges of the swamp meadow, in narrow areas that have not been too much disturbed by cultivation, true meadow

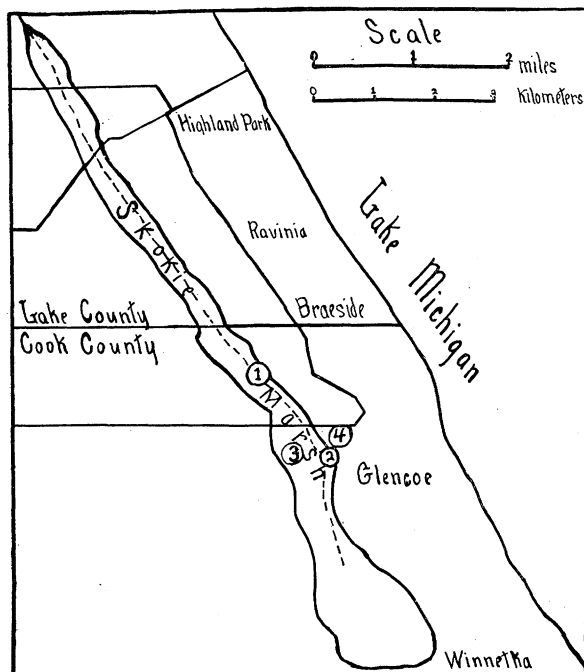


FIG. 1.—Map of Skokie Marsh; the dotted line represents Skokie Stream

is commonly present. At certain places, however, there is an abrupt transition from swamp meadow to forest.

In the reed swamp the plants belong to five easily recognized associations. Where the stream is deepest (as in fig. 2), aquatic or amphibious species, such as *Myriophyllum humile*,<sup>3</sup> *Ranunculus delphinifolius*, and *Potamogeton (zosteraefolius?)*, are common near the center. In the shallower parts, the species are supple-

<sup>3</sup> All plant names given in this paper conform with the nomenclature of GRAY's Manual, 7th ed., 1908.

mented or replaced by *Polygonum Muhlenbergii*, *P. hydropiperoides*, *Veronica Anagallis-aquatica*, *Radicula aquatica*, *Sium cicutaeifolium*, *Sparganium eurycarpum*, *Glyceria septentrionalis*, *Alisma Plantago-aquatica*, *Rumex verticillatus*, *Callitriche heterophylla*, and *C. palustris*. As *Polygonum hydropiperoides* and *Sium cicutaeifolium* are among the most abundant stream plants and appear to be dominant, we may classify the plants growing in the stream or upon its bed,



FIG. 2.—Skokie Stream at point west of Braeside, looking north; July

except along the margins, as the *Sium-Polygonum* association; using SCHOUW's method of nomenclature (SCHOUW 14, pp. 148–150), we shall call this the *Sio-polygonetum*. On either side of the *Sio-polygonetum* a narrow or sometimes broad girdle<sup>4</sup> of *Nymphaea advena* and *Castalia odorata* occurs in many places along the stream. Usually these species are accompanied by species characteristic of the *Sio-polygonetum*; but the soil and light conditions present in

<sup>4</sup> The word "girdle" is here equivalent to the "zones" of many recent authors, and conforms with the recent proposal of FLAHAULT and SCHRÖTER (5), except that it is here used for "bands" that are not "concentric."

the girdles of *Nymphaea* and *Castalia* are peculiar to them and justify their treatment as a separate association, the *Nymphaeetum*. Landward from the *Nymphaeetum* are found dense and either intermixed or almost pure growths of *Typha latifolia*, *Sparganium eurycarpum*, *Scirpus fluviatilis*, and *S. validus*. Scattered to a varying extent among these species are *Sagittaria latifolia* and *Sium cicutaeifolium*. Here and there are a few isolated patches of *Dulichium arundinaceum* and of *Decodon verticillatus*. This



FIG. 3.—Skokie Stream at point west of Glencoe, looking south; July

association will be referred to as the *Scirpo-typhetum*. Then again, in certain parts of the reed swamp, at stations slightly less hydrophytic, *Phragmites communis* is prominent. It forms exceedingly compact, nearly pure colonies that may reasonably be treated as an association, the *Phragmitetum*. Finally, we must mention the many large but somewhat scattered patches of *Iris versicolor* and *Acorus Calamus*, occurring in the outer parts of the reed swamp and often extending into the swamp meadow formation. These constitute an association of a very definite stamp, the *Iridoacoretum*.

A general comparison of the reed swamp associations shows that in the Sio-polygonetum and Nymphaeetum, where hydrophytism is greatest, the dominant plants are dicotyledonous. In fact, of the 15 species found to any appreciable extent in these two associations, the 10 most abundant (*Sium*, *Polygonum hydropiperoides*, *P. Muhlenbergii*, *Nymphaea*, *Castalia*, *Rumex*, *Veronica*, *Myriophyllum*, *Callitriche palustris*, and *C. heterophylla*) are dicotyledons.<sup>5</sup> In the other three associations the most abundant species are chiefly monocotyledons.

The swamp meadow differs from the reed swamp in being more uniform, due to greater parallelism between the water table and the soil surface, and does not admit of logical subdivision into associations. The plants are principally such grasses as *Calamagrostis canadensis*, *Glyceria nervata*, *Phalaris arundinacea*, *Poa triflora*, *Sphenopholis pallens*, and *Agrostis perennans*. These are frequently interspersed with *Carex lupuliformis*, *C. vesicaria monile*, *Scirpus atrovirens*, and *S. Eriophorum*. The swamp meadow is used by farmers of the district for the production of marsh hay, and many of them customarily burn over the areas in late autumn. Most of the shrubs and young trees are killed in this way, and so forest development is hindered. Trees occur only in small groups, consisting chiefly of *Salix* (*S. nigra* and other species), *Fraxinus americana*, and *Populus tremuloides*. Frequently associated with these are such shrubs as *Cornus stolonifera*, *Cephalanthus occidentalis*, and *Sambucus canadensis*.

Throughout the reed swamp and swamp meadow are many species which, though very abundant, share only to a small extent in giving to the several associations their distinctive appearance. Thus, *Ludwigia palustris*, *Proserpinaca palustris*, *Penthorum sedoides*, and *Stenophyllus capillaris* are low in habit and obscured by taller plants in the shade of which they may thrive. Again, *Aster Tradescanti*, *Boltonia asteroides*, *Lobelia cardinalis*, *Teucrium occidentale*, and *Scutellaria galericulata*, while extremely common, are nevertheless conspicuous only during the latter part of the summer. The names of such species will be given in this paper only where occasion demands.

<sup>5</sup> See HENSLOW (7), however, regarding the supposed monocotyledonous nature of *Nymphaea* and *Castalia*.

The meadow formation, as already stated, is narrow and more or less interrupted. The soil surface slopes mildly upward, away from that of the swamp meadow. The vegetation is much diversified at different places and from month to month during the vegetative season. *Poa pratensis* and *Agrostis alba* are the dominant grasses, but *Danthonia spicata* and *Agropyron caninum* are frequent. Scattered among the grasses are *Carex stipata*, *C. vulpinoidea*, *C. scoparia*, and *Eleocharis palustris*. In some parts of the meadow *Viola cucullata*, *Senecio aureus*, and *S. Balsamitae* are conspicuous in May and June, while later such species as *Lilium canadense* and *Rudbeckia hirta* are the most noticeable.

In the entire marsh there were found, exclusive of shrubs and trees, 163 species of pteridophytes and spermatophytes. Of these, 68 were common or even abundant.

### Certain ecological factors

Four Livingston atmometers were set out May 21, 1911, at different stations indicated in fig. 1. Readings were taken weekly from May 21 to October 15, and afterward corrected according to the method outlined by LIVINGSTON (9, p. 273, and 11).<sup>6</sup> A detailed account of the evaporation data thus obtained may be published subsequently elsewhere, but only the general results will be given here. It was found that the average daily evaporation at station 1 (in the center of the reed swamp) for the 147 days was 3 cc.; at station 2 (in the outer part of the reed swamp), 4.5 cc.; at station 3 (in the swamp meadow), 4.27 cc.; and at station 4 (in a stretch of forest running along the east side of the marsh and composed chiefly of *Quercus bicolor* and *Fraxinus americana*), 7.91 cc. Thus it will be seen that the evaporation rate was lowest in the reed swamp; that the evaporation rates in the reed swamp and the swamp meadow were closely similar; and that these rates were from about 38 per cent to about 57 per cent as great as the rate in a neighboring forest of *Quercus bicolor* and *Fraxinus americana*.

<sup>6</sup> The unglazed portion of each cup was placed at a mean height of 2.5 dm. above the soil surface. The instruments were not provided with a rain-excluding device, such as that recommended by LIVINGSTON (10).

From September 3 to October 22, 1911, weekly readings were taken of the rates of evaporation at different levels above the soil surface. Among the plants of *Phragmites*, four atmometers were placed at levels ranging from 0 m. to 1.95 m. above the soil. The average daily rate for the seven weeks at 1.95 m., or near the top of the *Phragmites* plants, was found to be 7.5 cc., just three times as great as the average daily rate of 2.5 cc., at the surface of the soil. Similar results were obtained with five atmometers in a dense growth of *Typha*. In each case the data secured are found to support YAPP's important contention (20) that for species growing side by side, but vegetating mainly at different heights, the conditions of growth may be very unlike.

The depth of the water table in the reed swamp and the swamp meadow was observed each week from May 21 to October 22, 1911. The water in Skokie Stream was about 1 m. deep in May; its depth then gradually decreased until in July, when the stream bed was in most places fairly dry; in August the water began to rise again, and by October had reached an average depth of about 1.1 m. In the rest of the reed swamp and in the swamp meadow the water table during May was coincident with or above the soil surface; in early September it sank to the maximum depth of 1 m. in the reed swamp and 1.75 m. in the swamp meadow; and then, rising rapidly, reached the surface again by the middle of October. According to farmers in the vicinity of Glencoe, Skokie Stream has sometimes in the past risen until a depth of about 3 m. was reached; in such cases the entire marsh was of course deeply submerged. Various attempts have been made to classify the constituent species of a formation with relation to the optimum water table depth for each species. But where the water table varies greatly in depth from month to month and from year to year, data must be secured through many years if they are to show more than merely the relative degrees of hydrophytism to which plants in different places are subject.

Litmus tests each week, from May 21 to October 22, 1911, showed the water in Skokie Stream to be either neutral or slightly alkaline. Similar tests showed the soil water in the outer parts of the reed swamp and in the swamp meadow to be usually neutral or slightly



alkaline; only for a few days in August was acid present, and then the amount was almost negligible.

### Subterranean organs and their interrelationships

A study of the subterranean organs of the reed swamp plants showed that in many cases the depth is roughly proportionate to the depth of the water table. YAPP (19) arrived at a similar conclusion concerning the plants at Wicken Fen. And since the depth of the water table may influence the depth of the subterranean

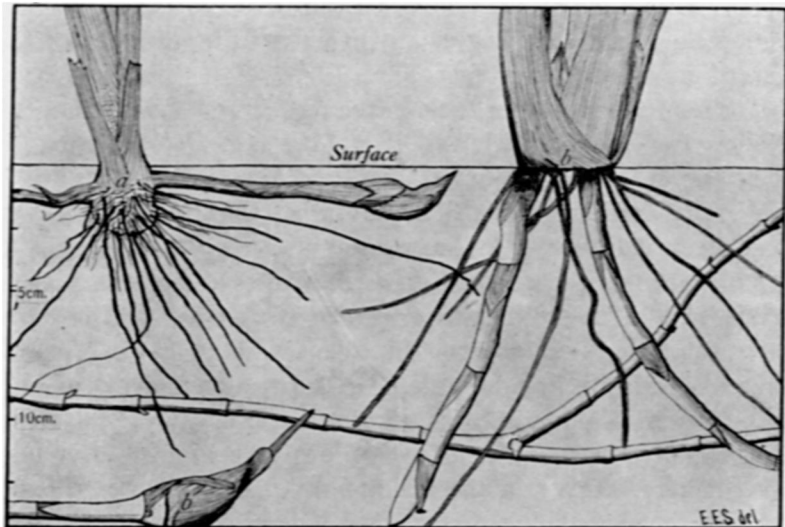


FIG. 4.—a, *Sparganium eurycarpum*; b, *Sagittaria latifolia*; c, *Polygonum Muhlenbergii*; July.

organs, the latter in turn may enter as a potent factor into the success or failure of various species. Thus, for example, the rhizomes of *Polygonum Muhlenbergii*, where this species occurs in the Sio-polygonetum, are usually at or near the surface of the stream bed. As KING (8, p. 240) and others have pointed out, saturated soil like that of the stream bed does not admit oxygen freely. And so, in the Sio-polygonetum, the rhizomes of *Polygonum* and their roots appear advantageously placed. But in the Scirpophysetum (fig. 4), where the surface soil is occupied by an extremely dense mat composed of the rhizomes of *Typha*, *Sparganium*, and

*Scirpus*, the rhizomes of *Polygonum* average about 10 cm. in depth. Hence in the Scirpo-typhetum, although the rhizomes of *Polygonum* are lower, evidently, in response to the greater average depth of the water table, they gain the additional advantage of being able to travel with less interference from the other rhizome systems.

An examination of *Typha*, *Sparganium*, *Scirpus fluviatilis*, and *S. validus* shows these species to be very similar in growth-form and hence capable of keen competition. Where any one of these species becomes more abundant in the Scirpo-typhetum, the others become less so. Because of the thick, strong rhizomes, the subterranean competition is to some extent mechanical; but, as CLEMENTS (3, pp. 285-289) maintains, it is probably to a much greater extent physiological (or "physical"), especially in the case of the roots proper. The opposition that any or all of these species can offer to the intrusion of other species makes their hold upon the soil very effective. With *Sagittaria* (fig. 4), however, the case is different. Its growth-form favors a less compact arrangement of the individual plants. Its rhizomes cannot produce a thick mat. Obviously, as the plants of *Sagittaria* are developing vegetatively, other species, such as *Typha*, *Sparganium*, and *Scirpus*, may easily invade and occupy the soil with their densely matting rhizomes. Subsequently the rhizomes of *Sagittaria*, if they are to establish new plants at proper distances away from the parent plant, must either plough their way along through the surface mat of rhizomes or travel underneath. They usually do the latter. As a rule several rhizomes start growth from each plant in early summer, in a downward direction; at a depth of 10-15 cm. they assume a horizontal direction for some distance; they then grow upward again, with a tuberous, propagative thickening near the distal end, and finally resemble somewhat a shallow, inverted arch.<sup>7</sup> Thus interference from surface rhizomes and roots is to a great extent avoided. In this case, then, while it is not certain that the inverted arch of the *Sagittaria* rhizome is a direct adaptation to this particular struggle, it is certain that the inverted arch, however induced originally, is here of the greatest value.

<sup>7</sup> For illustrations of the similar rhizomes of *Sagittaria sagittifolia* see GLÜCK (6, pl. 6 and figs. 35 and 39).

PIETERS (13) found among the plants of western Lake Erie that even where *Sagittaria latifolia* was most abundant, *Sparganium* (and *Zizania*) had secured a foothold. On the other hand, throughout all the broad "zones" of *Sparganium*, *Scirpus validus* ("*S. lacustris*"), and *S. fluviatilis* that he describes, he says *Sagittaria latifolia* was common.

A study of the subterranean organs of *Sagittaria*, *Sparganium* (or *Typha* or *Scirpus*), and *Polygonum* shows that because of differences in direction or in depth they conflict but little. Again, because of differences in growth-form, their aerial parts do not conflict seriously. Thus a given area can usually support a greater mass of vegetation if these three growth-forms be present in fair mixture than if only one be present. SPALDING (15) has described the mutual relationships of *Cereus giganteus* and *Parkinsonia microphylla*, two desert species which thrive together because the occupation of different depths by their root systems enables them "to utilize to the utmost the scanty rainfall." WOODHEAD (18) found *Holcus*, *Pteris*, and *Scilla* forming a non-combative "society or sub-association." For a group of plants mutually competitive, WOODHEAD uses the term "competitive association." Recently WILSON (17) likewise speaks of a "complementary association" or "society." But the use of the words "association" and "society" in this connection is unfortunate. These words have already been used by COWLES (4) and others (see WARMING 16, p. 144) to denote a primary subdivision of a formation. As will be seen later (and in fact as WOODHEAD's use interchangeably of "sub-association" and "association" would imply), not all complementary or competitive groups are coextensive with a true association. We shall here substitute the word community, which is of less restricted application. Thus, *Sagittaria* and *Polygonum*, where occurring in the Scirpo-typhetum with either *Typha* or *Scirpus fluviatilis* or *S. validus*, constitute a complementary community. But *Sparganium*, *Typha*, *Scirpus fluviatilis*, and *S. validus*, where they occur intermixed, form a competitive community.

Species that are complementary in one association may be less so in another. Thus, *Polygonum Muhlenbergii* and *Sparganium* are complementary in the Scirpo-typhetum; but in the Sio-

polygonetum, where their rhizomes lie in common near or at the surface of the stream bed, they are "edaphically" (see WOODHEAD 18) competitive, and hence complementary only in an aerial way. In this particular case, however, the frequently open appearance of the vegetation in the Sio-polygonetum indicates that the mutual biotic struggle of the two species is less keen than their separate struggles against somewhat adverse environmental conditions.

In the reed swamp certain mints become conspicuous during midsummer, particularly so in the Scirpo-typhetum, where they thrive in the shelter of *Typha* and other tall plants. *Teucrium occidentale* and *Scutellaria galericulata* are very common. They produce from their basal nodes numerous slender stolons that run out at different depths in the soil, and these stolons may produce new plants. These species tend to have their root systems 3-6 cm. lower in wet situations than in dry, although exceptions to this rule are not rare. But whether growing from plants in dry or from those in wet situations, the new stolons exhibit a remarkable power of changing their direction of growth, in response to numerous obstructions, and thus they may proceed further without serious results. Considering the strength and size of the rhizomes of *Typha*, *Sparganium*, and *Scirpus*, also the delicate nature of the stolons of *Teucrium* and *Scutellaria* and their capacity for altering growth-direction, it is probable that mechanical competition between such rhizomes as those of *Typha* and such stolons as those of *Teucrium* is practically absent. Again, the aerial parts of the *Typha* form vegetate chiefly in higher atmospheric strata than do those of the *Teucrium* form. Evaporation readings show that in the higher strata evaporation is much greater. And while plants of relatively xerophytic structure (e.g., *Typha*, *Sparganium*, and *Scirpus*) are fitted to withstand acute drying conditions, plants with foliage of looser texture (e.g., *Teucrium* and *Scutellaria*) can vegetate better in lower strata where the effect is that of greater humidity; the abundance of the latter plants among the former at Skokie Marsh tends to confirm this statement. Further, the persistence with which tall plants like *Typha* become dominant under favorable soil conditions shows that they are not, at least noticeably, harmed by plants like *Teucrium*. If, finally, we allow for the great avail-

ability of nitrogenous foods in the soil and for the differences in food requirements, it becomes clear that the numerous communities of *Typha* and *Teucrium*, *Typha* and *Scutellaria*, *Sparganium* and *Teucrium*, etc., are complementary.

The purity of the *Phragmitetum* has already been mentioned. Many species that flourish elsewhere in the reed swamp under a wide range of light, moisture, and other shelter conditions fail to thrive here. Only *Calamagrostis canadensis* gains noticeable

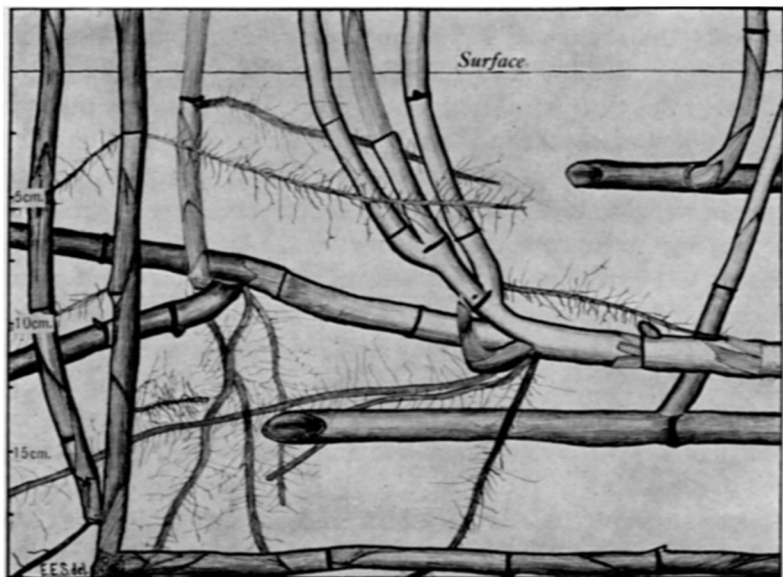


FIG. 5.—*Phragmites communis*; July

entrance, and then imperfectly. The dead *Phragmites*' growth of previous years makes a considerable but loose covering near the soil, its decay not being facilitated as in the *Scirpo*-typhetum, where water is more abundant. This dead cover may perhaps act as a partial check upon the invasion of other species. But a study of the rhizomes of *Phragmites* (fig. 5) shows another fact which probably is more important. They do not occupy one particular level, but rather several different levels of soil. As a result, there is formed a dense mat of rhizomes and roots, about 2.5 dm. deep. Obviously, the subterranean organs of other species which might

start growth here must compete with the extraordinarily large number of *Phragmites* roots and rhizomes. Where other factors are suited equally to *Phragmites* and to competing species, this biotic factor in the subaerial struggle ought usually to decide in favor of *Phragmites*.

The Nymphaeetum displays many complementary communities. The rhizomes of *Nymphaea advena* (fig. 6) are usually

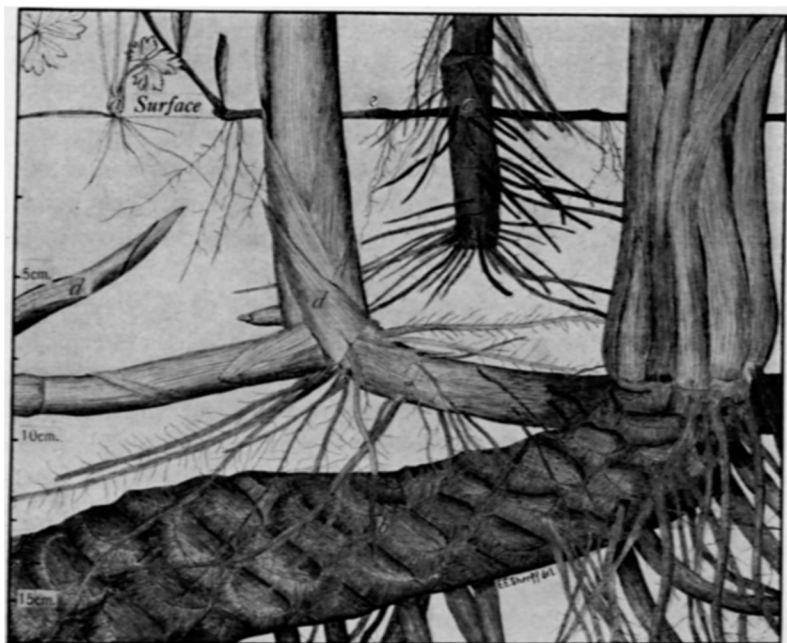


FIG. 6.—a, *Ranunculus delphinifolius*; b, *Nymphaea advena*; c, *Sium cicutaefolium*; d, *Typha latifolia*; e, *Polygonum hydropiperoides*; drawn in early July.

5–10 cm. thick and lie mostly at a depth of 8–25 cm. below the soil surface. The rhizomes of *Castalia odorata*, while smaller, lie at a similar depth. Where the Nymphaeetum intergrades with the Scirpo-typhetum, as is commonly the case, the rhizomes of *Typha*, *Sparganium*, and *Scirpus validus* lie higher in the soil. In many places the soil surface itself is occupied by the stolons of *Ranunculus delphinifolius* and the creeping stems of *Polygonum hydropiperoides*, with a large, upright stem base of *Sium cicutaefolium* present here

and there. In other places, *Ranunculus* is replaced by *Myriophyllum humile* or by young plants (growing chiefly from detached leaves) of *Radicula aquatica*, while *Polygonum* is replaced by *Veronica Anagallis-aquatica*, and *Sium* by *Rumex verticillatus*. And while it is true that *Nymphaea* and *Castalia*, or *Typha* and *Sparganium* and *Scirpus*, or *Ranunculus* and *Myriophyllum* and *Radicula*, or *Polygonum* and *Veronica*, or *Sium* and *Rumex* are mutually competitive, yet a complete community (as shown, e.g., in fig. 6) is complementary; the basal parts chiefly because of different depths, and the upper parts chiefly because of different growth-forms.

An inspection of the *Nymphaeetum* shows that only where *Nymphaea* is nearly or quite absent does *Sagittaria latifolia* successfully invade from the *Scirpo-typhetum*. As is commonly known, the rhizomes of *Nymphaea* in many habitats are usually decayed to within a short distance of the growing apex. An investigation during August 1911 showed that generally where the rhizomes of *Sagittaria* had penetrated these decayed parts, they themselves had started to decay.<sup>8</sup> Frequent cases were found where the decayed *Nymphaea* rhizomes lay nearer the surface and the *Sagittaria* rhizomes had proceeded underneath, unharmed. Speaking in a general way, while *Nymphaea* and *Sagittaria* thrive better in the *Nymphaeetum* and *Scirpo-typhetum* respectively, yet along the line of tension between these two associations the injury done by the decayed *Nymphaea* rhizomes to the rhizomes of *Sagittaria* is a factor that appears to be decisively in favor of *Nymphaea*. The inverted rhizome arch of *Sagittaria*, useful in the *Scirpo-typhetum*, is here more often harmful.

In many parts of the *Irido-acoretum*, *Polygonum Muhlenbergii* and *Galium Claytoni* abound, and these form with *Acorus* a complementary community (fig. 7). The creeping stems of *Galium* root upon the soil surface, the rhizomes of *Acorus* lie just beneath, and those of *Polygonum* are deepest of all. The bushy shoot of *Galium* appears not to harm the slender, ensiform leaves of *Acorus*, and

<sup>8</sup> Many litmus tests uniformly showed the decayed parts of the *Nymphaea* rhizomes to be strongly acid. Enough cultural experiments have not been performed, however, to determine whether the effect upon the *Sagittaria* rhizomes, as above noted, is due to acid or to other causes.

they in turn do little harm to it. In late summer, the shoots of *Polygonum* rise above those of *Acorus* and *Galium* without apparent harm to either of them. And while *Polygonum* might increase in abundance if *Acorus* and *Galium* were entirely absent, still to a great extent the community, viewed as a whole, is complementary. Elsewhere in the Irido-acoretum the rhizomes of *Acorus* are replaced by those of *Iris*; and very often the rhizomes of *Galium* are replaced by those of *Ludwigia palustris*, *L. polycarpa*, *Proserpinaca*

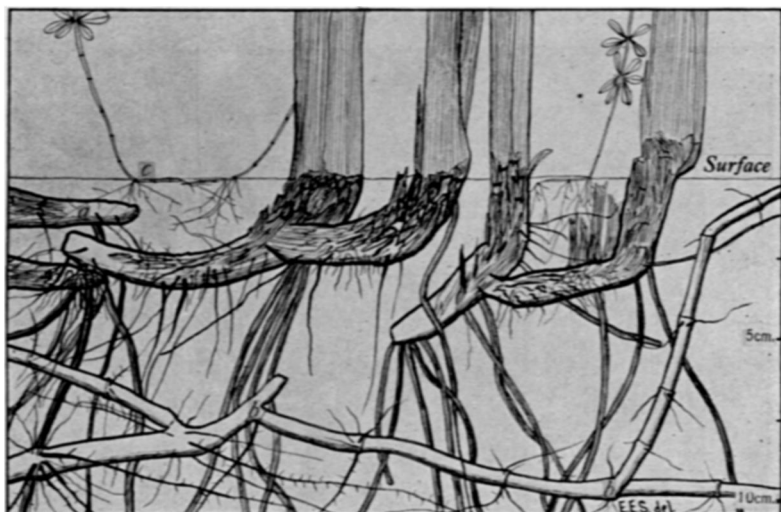


FIG. 7.—a, *Acorus Calamus*; b, *Polygonum Muhlenbergii*; c, *Galium Claytoni*; July

*palustris*, *Penthorum sedoides*, *Veronica scutellata*, or *Campanula parinoides*.

The basal parts of the various swamp meadow species are usually more slender than those of the reed swamp species, and hence the texture of the surface mat of rhizomes, roots, etc., is finer. Then, too, reproduction by seeds becomes more common. *Polygonum Muhlenbergii* is present in the swamp meadow, and by means of its extensively creeping rhizomes, which lie rather low, it forms in some places large patches. Certain other perennials, e.g., *Asclepias incarnata* and *Sium cicutaefolium*, which root near the surface, may reproduce largely by seed or by new shoots arising from the old stem base of the preceding year. In the middle



and latter parts of the summer, when the surface soil is no longer saturated with water, such annuals as *Panicum capillare*, *Echinochloa Crus-galli*, *Eragrostis hypnoides*, *Stenophyllus capillaris*, *Polygonum Persicaria*, *Amaranthus paniculatus*, and *Erechthites hieracifolia* take possession of all exposed surface soil and become exceedingly abundant. Much of the surface soil that has been denuded by burning or by other causes is already occupied, however, by the rhizomes of perennials such as *Ludwigia palustris*, *L. polycarpa*, *Proserpinaca palustris*, etc. In these cases *Boltonia*

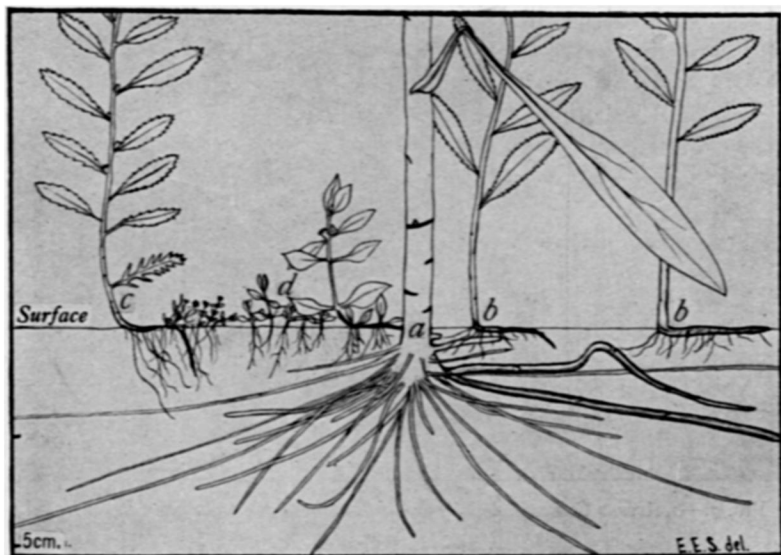


FIG. 8.—a, *Boltonia asteroides*; b, *Penthorum sedoides*; c, *Proserpinaca palustris*; d, *Ludwigia palustris*; e, *Callitriche palustris*; July.

*asteroides*, *Callitriche heterophylla*, and *C. palustris* are often abundant; both species of *Callitriche*, however, die away in midsummer, becoming replaced by annuals. Fig. 8 shows such a community. *Callitriche*, maturing earliest, is “seasonally” (WOODHEAD 18) complementary with the other species. *Boltonia* roots lowest, while its aerial shoot grows much the highest; and since it is not harmed very much by *Proserpinaca*, *Ludwigia*, and *Penthorum*, while they derive, if anything, benefit from its shelter, *Boltonia* is complementary both aerially and subaerially. *Proserpinaca*,

*Ludwigia*, and *Penthorum* are very similar throughout in growth-form and they constitute mutually a competitive community. But, even though mutually competitive, they form with *Boltonia* and *Callitriche* a community that may properly be called complementary.

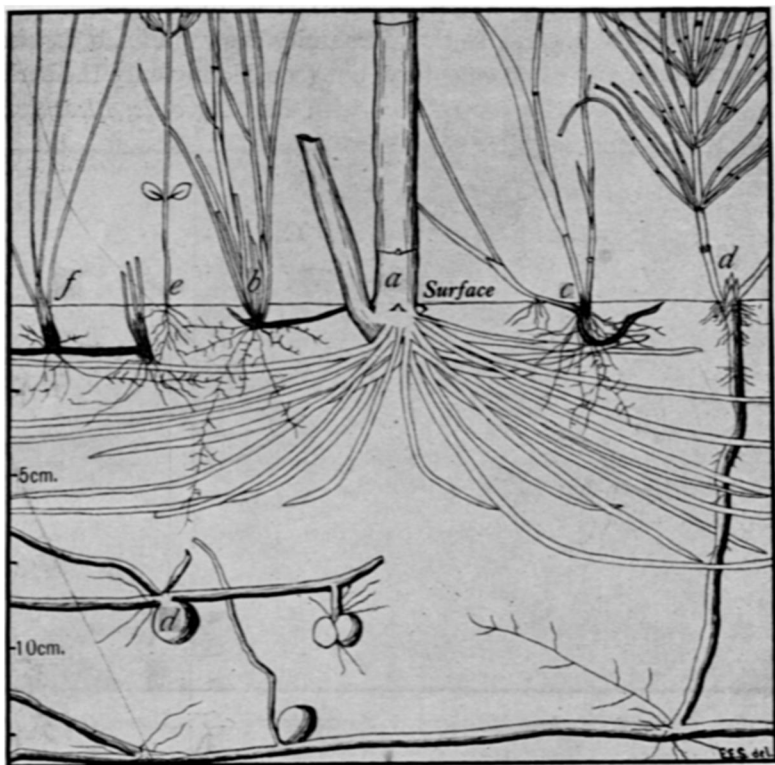


FIG. 9.—a, *Asclepias incarnata*; b, *Poa pratensis*; c, *Agrostis alba*; d, *Equisetum arvense*; e, *Acalypha virginica*; f, *Eleocharis palustris*; July.

As has already been stated, the flora of the meadow is highly diversified. A very large number of definite interrelationships, similar to those detailed for the reed swamp and the swamp meadow, are found to exist, but lack of space precludes more than a brief description of a few examples. In the moist parts of the meadow, the soil at a depth of 3–12 cm. frequently contains the tuberous thickened roots of *Cicuta maculata* and *Oxypolis rigidior*, also the

tuber-bearing rhizomes of *Equisetum arvense*. In drier situations the bulbs of *Lilium canadense* occur at a similar depth (most often about 10 cm. deep). Higher in the soil may be found (fig. 9) roots of such species as *Asclepias incarnata*, *Thalictrum revolutum*, and *Lathyrus palustris*, while the surface soil contains a mixture of the root systems of *Poa pratensis*, *Agrostis alba*, *Eleocharis palustris*, *Acalypha virginica*, etc. In the community shown in fig. 9, *Equisetum* is edaphically complementary, but (considering only the aerial sterile shoots) aerially competitive with *Poa*, *Agrostis*, *Eleocharis*,

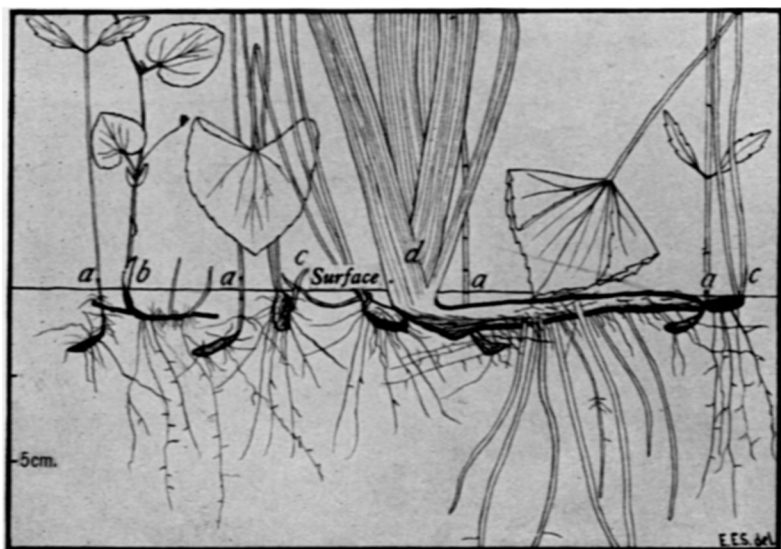


FIG. 10.—a, *Lycopodium americanus*; b, *Viola conspersa*; c, *Viola cucullata*; d, *Iris versicolor*; July.

and *Acalypha*. To a moderate extent, the plants rooting near or at the surface appear to be complementary with the plants rooting deeper.

Small, apparently open depressions are numerous in the moist parts of the meadow. These generally contain (fig. 10) such plants as *Iris*, *Acorus*, *Viola conspersa*, *V. cucullata*, *Cardamine bulbosa*, and seedlings of *Lycopodium americanus*. And while the rhizomes of *Cardamine* and *Lycopodium* occur almost invariably just below those of the other species, and while the different species doubtless make

different demands upon the soil, yet edaphic competition is undoubtedly sharp. The almost complete absence, in these small areas, of stoloniferous or loosely spreading species makes it seem certain that there exists some mechanical competition in which species of compact and frequently caespitose habit or species capable of reproducing extensively from seed are successful. The extent, however, to which their success is achieved because of their growth-form or because of their superior adaptation to the particular complex of soil and moisture conditions in these small areas is of course incapable of accurate estimation without further study. The idea of mechanical competition (i.e., a struggle either among the various species because of the mutual bodily resistance of any or all of their growing parts, or of individual species because of the resistance offered by the soil's compactness to the locomotion of their subterranean organs) is opposed by CLEMENTS (3, pp. 285-289); but WARMING (16, p. 324), in accounting for the usual absence of vegetative locomotion among perennial herbs of the meadow formation, seems inclined to accept this idea in part.

### Summary and conclusions

1. Atmometer readings, taken for seven weeks at four different levels among *Phragmites* plants and at five different levels among *Typha* plants, show that among marsh species of compact social growth evaporation is proportionate to the height above the soil. These results thus coincide with those of YAPP (20).

2. Data accumulated at Skokie Marsh appear to support the conclusion of MASSART (12) that it is a matter of importance to perennial plants that their hibernating organs occupy a definite level in the soil.

3. Certain observed cases of variation in this level (*Teucrium occidentale*, *Polygonum Muhlenbergii*, etc.), corresponding to changes in the water level, indicate that with certain species, at least, the depth of the water table is much the most potent controlling factor.

4. Two or more species may live together in harmony because (1) their subterranean stems may lie at different depths; (2) their roots may thus be produced at different depths; (3) even where roots are produced at the same depth, they may make unlike

demands upon the soil; (4) the aerial shoots may have unlike growth-forms; or because (5) even where these growth-forms are similar, they may vegetate chiefly at different times of the year. According as one or more of these conditions control the floristic composition of a given community the community may be called complementary.

5. The root depth having been determined by various factors for the different species in a community, the specifically different root systems then function in a complementary or a competitive manner as the case may be. But even if the root systems be complementary, the community may be competitive because of marked competition among the aerial parts. Likewise, competitive root systems may render competitive a community otherwise complementary.

6. Through the ability of certain species to utilize different strata in the soil, the aerial portions of these plants are brought into a closer competition. And with closer competition, the chances in the past for further adaptation of similar aerial shoots to dissimilar growth conditions must have been greatly increased. Hence communities, formerly complementary in a purely edaphic way, may have been largely instrumental in the evolution of completely complementary communities. In so far as they have been thus instrumental, the fact deserves great emphasis, especially when we consider the far-reaching changes in form and anatomical structure necessarily developed as a prerequisite to living in a completely complementary community.

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